

Binocular rivalry: A time dependence of eye and stimulus contributions

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In binocular rivalry, the visual percept alternates stochastically between two dichoptically presented stimuli. It is established that both processes related to the eye of origin and binocular, stimulus-related processes account for these fluctuations in conscious perception. Here we studied how their relative contributions vary over time. We applied brief disruptions to rivalry displays, concurrent with an optional eye swap, at varying time intervals after one stimulus became visible (dominant). We found that early in a dominance phase the dominant eye determined the percept by stabilizing its own contribution (regardless of the stimulus), with an additional yet weaker stabilizing contribution of the stimulus (regardless of the eye). Their stabilizing contributions declined in parallel with time so that late in a dominance phase the stimulus (and in some cases also the eye-based) contribution turned negative, favoring a perceptual (or ocular) switch. Our findings show that depending on the time, first processes related to the eye of origin and then those related to the stimulus can have a greater net influence on the stability of the conscious percept. Their co-varying change may be due to feedback from image- to eye-of-origin representations.

Keywords: binocular rivalry, consciousness, flash suppression, onset rivalry, monocular, perception

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Introduction

Binocular rivalry is a puzzling phenomenon: when two distinct images are presented to the eyes, the percept changes stochastically from one image to the other, despite the unchanged stimulation of the eyes. This makes rivalry paradigms well suited to study the neural sources of conscious perception (Blake & Logothetis, 2002).

Early evidence pointed to monocular channels influencing the percept. For example, when stimuli were exchanged between the eyes after one stimulus gained perceptual dominance, the percept tended to follow the dominant eye (Blake, Westendorf, & Overton, 1980). Similarly, when one eye was cued prior to a rivalry display, the stimulus shown to it was more likely to become visible (dominant) subsequently (Ooi & He, 1999).

However, the nature of holistic stimuli also influences dominance. When a patchwork of two images was presented to one eye and the complementing patchwork to the other eye, observers tended to perceive the coherent combination image (Diaz-Caneja, 1928, translated by Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovacs, Pappathomas, Yang, & Feher, 1996). Similarly, rapid

swapping of stimuli between eyes can lead to one dominant percept across several swaps (Logothetis, Leopold, & Sheinberg, 1996). Together, the evidence shows both eye-based and stimulus-based influences on rivalry.

Indeed, the depth of suppression may depend on the amount of shared neural substrate between the two stimuli, with, e.g., two face stimuli leading to greater suppression than a motion vs. face stimulus, or two simple grating stimuli (Alais & Melcher, 2007; Knapen, Kanai, Brascamp, van Boxtel, & van Ee, 2007). In addition, there is good evidence that eye-based and image-based contributions may influence each other (Ngo, Liu, Tilley, Pettigrew, & Miller, 2007; van Boxtel, Alais, & van Ee, 2008; Watson, Pearson, & Clifford, 2004). For example, two point-like walkers rival when each is presented to a different eye, but not when they are presented in an eye-scrambled way (Watson et al., 2004).

Several paradigms showed that the eye-based contribution to suppression may be stronger than stimulus suppression: first, visual probes or TMS over early visual areas revealed a deeper suppression during conventional rivalry compared to swap rivalry (Bhardwaj, O'Shea, Alais, & Parker, 2008; Pearson, Tadin, & Blake, 2007).

Second, global stimulus differences alone do not induce rivalry unless there are also interocular differences (Carlson & He, 2004). Third, even in paradigms probing the so-called “stimulus memory” (i.e., the return to the same percept after a rivalrous stimulus was hidden over several seconds), a strong eye-based contribution was found, with a weaker but significant contribution of binocular factors such as color or orientation (Chen & He, 2004; Leopold, Wilke, Maier, & Logothetis, 2002; Pearson & Clifford, 2004).

All in all, it is thus widely accepted that both eye-based and stimulus-based processes influence perceptual dominance during rivalrous displays. However, it is not known how or whether their separate contributions vary over time, and if both vary in the same way. An understanding of this is of particular interest, because it is the variation that accounts for perceptual dynamics. In this study, we attempt to quantify this dynamics within a single phase of dominance during binocular rivalry.

To test for time-varying contributions of eye- and stimulus-based factors, we induced dominance in a binocular rivalry setting and then interrupted the visual display with brief (100 ms) binocularly presented high contrast “interruption patterns” that do not favor either eye or percept. Such brief abrupt changes in either or both eyes can, but do not need to, alter dominance, and thus constitute a test for perceptual stability (Blake & Fox, 1974; Kanai, Moradi, Shimojo, & Verstraten, 2005; Wolfe, 1984). This interruption paradigm thus measured the relative strength of the stimuli, in terms of the probability of the dominant stimulus returning to dominance after the interruption. We applied these interruptions at varying time intervals (between 0.3 and 3 s) after one stimulus (and eye) had obtained dominance.

After the interruption pattern, the original rivalry stimuli were either maintained or exchanged between the eyes, and subjects indicated which stimulus they perceived. This allowed us to measure the extent to which perceptual stability was instilled by eye-related or by stimulus-related processes: when stimuli were not swapped, eye-of-origin- and stimulus-related processes would add to determine the perceptual outcome, and when stimuli were swapped, stimulus-related stability would contribute positively and eye-related stability negatively to the perceptual outcome.

As rivalry is characterized by stable dominance alternating with suppression, we expected initially stabilizing contributions early in a dominance phase to turn negative (destabilizing) over time. Because of the above-mentioned evidence indicating interactions between eye- and stimulus-based processes, our expectation was that both would vary over time in their stabilizing or destabilizing contributions, potentially reflecting an interaction. In addition to these time-evolving variations, we expected the static offsets of the eye-related and stimulus-related contributions to differ in different experimental settings. For example, the spontaneous rapid initial dominance of one

eye after the onset of dichoptic stimulus presentation (“onset rivalry”) is likely caused by strong eye-related factors (Carter & Cavanagh, 2007), in contrast to the widely used flash suppression paradigm in which the experimenter determines which eye becomes dominant (Wolfe, 1984). Similarly, the complex history of eye and stimulus dominances during continuous rivalry may lead to distinct results compared to the well-controlled flash suppression paradigm (Brascamp et al., 2008; Klink et al., 2008; Ngo et al., 2007).

We therefore applied our interruption paradigm in three rivalry settings—flash suppression (Wolfe, 1984), onset rivalry (Carter & Cavanagh, 2007), and continuous viewing—with delays of 0.3 s or 3 s after dichoptic stimulation onset (or after reports of perceptual changes, respectively; see Figures 1a, 2a, and 5a). Together with eye-swap or no-swap conditions, this yielded four independent experiments per rivalry setting.

Methods

Subjects and stimuli

Three different rivalry paradigms were used to study perceptual outcomes after the presentation of brief binocular interrupting patterns: flash suppression, onset rivalry, and continuous rivalry. In each experiment, the following number of subjects took part: 6 (3 females), 6 (2), and 8 (3), respectively, with 9 (4) in an additional flash suppression experiment using grating stimuli. All had normal or corrected-to-normal vision and were aged 24–34 years. All gave written informed consent, and the experiments were approved by the Joint Ethics Committee of the Max Planck Institute and the University Clinic Tübingen. In each experiment, all but one of the participants (AB) were naive with regard to the purpose of the experiment. All were well trained on binocular rivalry paradigms and had well-balanced dominances between the eyes: on average, the less dominant eye achieved $45.0 \pm 4.8\%$ (mean \pm SD) of the total stable viewing time (i.e., excluding piecemeal vision) in continuous rivalry experiments preceding the reported sessions.

Stimuli were generated using Cogent 1.27 (John Romaya, Wellcome Department of Imaging Neuroscience, University College London, www.vislab.ucl.ac.uk/CogentGraphics.html) on a Windows PC running MATLAB 2006b (Mathworks) and presented on independently linearized monitors that faced each other (resolution 1024×768 at 85 Hz). They were viewed through a set of angled front-surfaced silver-coated mirrors in a black-shielded setup (viewing distance: 118 cm).

Stimuli consisted of circularly cropped (outer 10% of radius cosine-smoothed runout) photographs of flowers of identical luminance (2.5 cd/m^2) and RMS contrast ($1.32 \pm 0.20 \text{ cd/m}^2$ (mean \pm SD; range: 0.99–1.65 cd/m^2),

a Flash suppression:

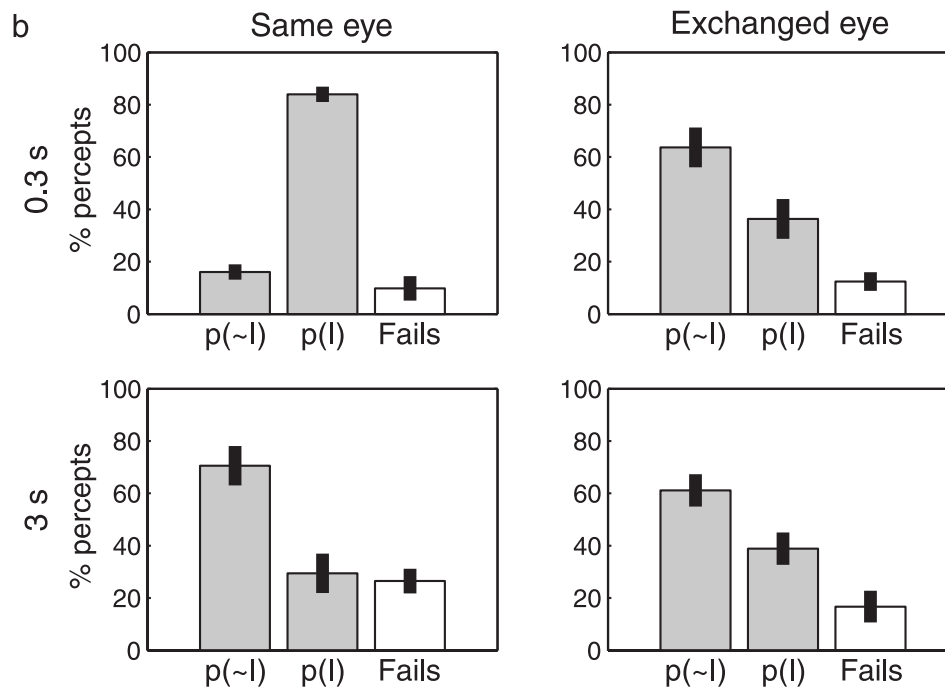
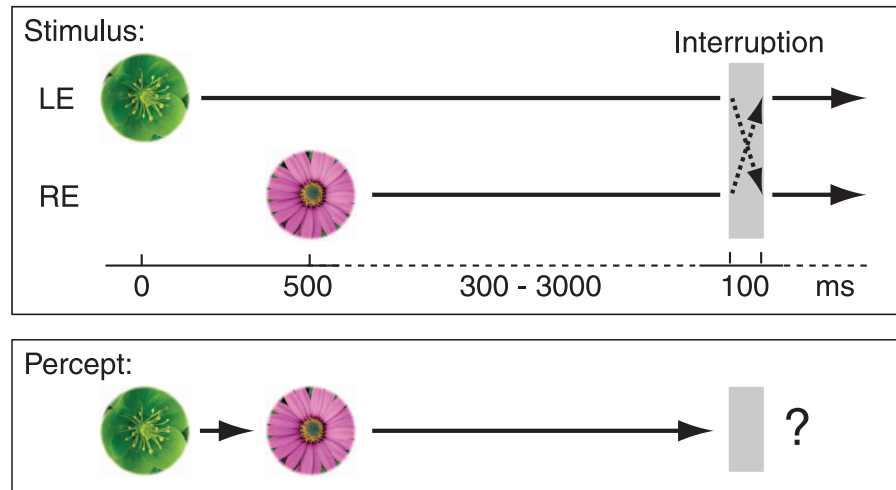


Figure 1. Stimuli and results of the flash suppression experiment. (a) Illustration of the flower stimuli and of the experimental paradigm used. Perceptual dominance was induced in the second eye by stimulating it 500 ms after the first eye (“flash suppression” (Wolfe, 1984)). After 0.3 or 3 s, a binocular interrupting pattern was presented to both eyes. In half the trials, stimuli were exchanged between the eyes during the interruption, thus dissociating dominant eye from dominant stimulus. Subjects indicated by button press which stimulus was perceived immediately following the interruption (see Methods section). (b) Percentages of percepts following the binocular interruption, for each of the four conditions. Filled bars show the percentage of valid trials where the same image was perceived after the interruption as before ($p(l)$) or where it changed ($p(\sim l)$)—note that $p(l) + p(\sim l) = 100\%$. “Fails” shows the percentage of failed trials (e.g., due to spontaneous switch or piecemeal rivalry). After short initial dominance (top row), perceptual switches are primarily dictated by the initially dominant eye. After long dominance (bottom row), percepts switch to the previously suppressed percept, with little influence of the eye of origin. Error bars: SE across six subjects.

Michelson: $\sim 100\%$) presented foveally and subtended 0.75 degrees (see examples in Figure 1a, and the full set of stimuli in Supplementary Figure S1). In an additional experiment, oriented gratings (± 45 deg, 5 cpd, 5.3 cd/m^2 , $64 \pm 27\%$ contrast (range: 50%–100%), tinted light green

($x: 0.274$, $y: 0.359$) or magenta ($x: 0.255$, $y: 0.255$) were shown instead of the flower stimuli. The small size minimized piecemeal rivalry, and the low luminance minimized afterimages. Stimuli were superimposed on an isoluminant gray circular annulus (3 deg diameter, CIE

a Onset rivalry:

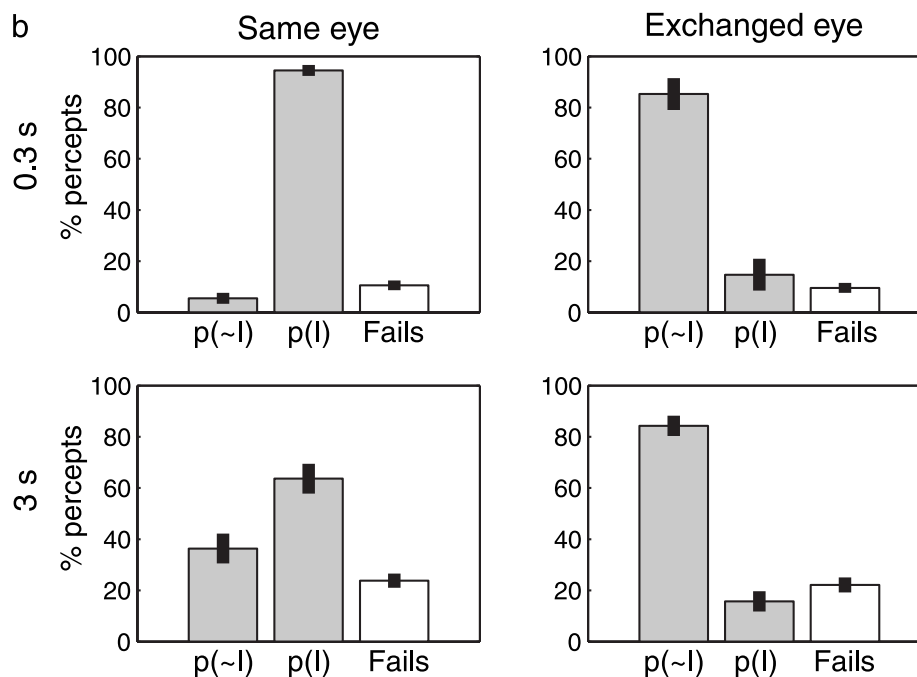
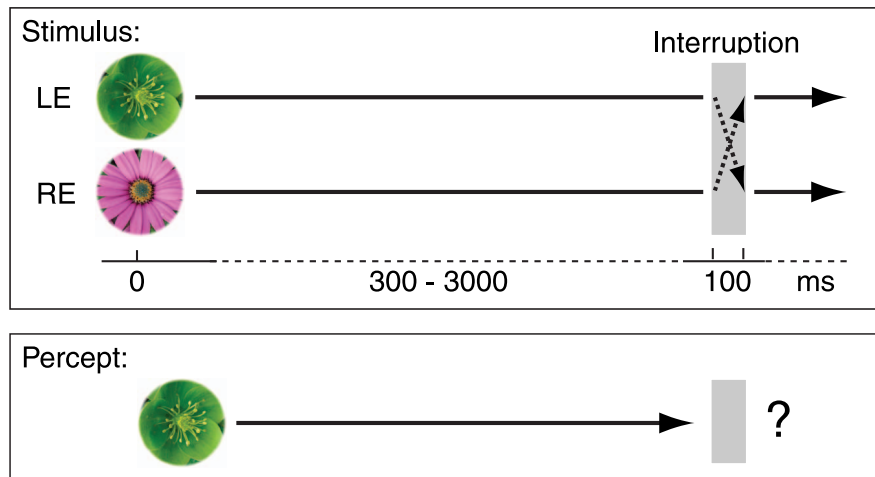


Figure 2. Stimuli and results of the onset rivalry experiment. (a) The same as in Figure 1, but here both eyes were stimulated simultaneously. Almost immediately, one stimulus gained dominance, and the interrupting pattern was shown 0.3 or 3 s after stimulus onset. (b) Similar results as in Figure 1, but with overall stronger stabilizing contributions of the initially dominant eye (i.e., positive offset of $p(l)$ in same-eye trials and of $p(\sim l)$ in exchanged-eye trials compared to Figure 1).

chromaticity: $x: 0.262$, $y: 0.291$) containing a thin black concentric circle (1 deg diameter, 0.04 deg thickness, 0.0 cd/m^2) with centrifugal crosshairs (extending to 3 deg), shown on an otherwise black screen. This was shown on both monitors along with a black and gray fixation cross (0.15 deg width, 0.075 deg thickness) at all times to facilitate binocular fusion. The interrupting pattern and the pretrial masks (0.75 deg diameter) consisted of white noise (randomly distributed gray-level pixel values between 0 and 7.5 cd/m^2) with 3.75 cd/m^2 (=150%) luminance and 100% contrast and were randomly selected from 10 precalculated white noise patterns for each

presentation. On- and offsets of stimuli happened instantaneously (from one frame to the next), with subjects reporting the perceived flower or orientation, respectively.

Rivalry paradigms

Each subject was accustomed to continuous and trial-based binocular rivalry on days prior to data collection, and pairs of flower stimuli were selected (from six flower stimuli) that led to balanced dominance (i.e., between 40% and 60% dominance time for a given flower of the

total dominance time, measured across both eyes). Stimulus contrasts were adjusted for each subject to achieve median dominance times of about 3–4 s in continuous rivalry. Note that the contrasts were identical for both stimuli used for a given subject in all experiments. Three rivalry paradigms were used as described below.

Flash suppression

Each trial began with a 3-s binocular mask (white noise, same properties as the interruption pattern), followed by a gray background for 2 s. As illustrated in [Figure 1a](#), then one stimulus (flower or grating) was presented to one eye (now dominant) for 500 ms, followed by the additional presentation of the other stimulus to the other eye (flash suppression; now dominant) for 300 or 3000 ms before presentation of the binocular interrupting pattern for 100 ms. Then both stimuli were either presented to the same eyes as before or exchanged, for 1500 ms (see [Figure 1a](#); [Supplementary Figure S2](#) illustrates each of the four conditions separately). Subjects reported the stimulus dominantly perceived immediately after the interruption by pressing one of two buttons. After the interruption, it was sufficient if one stimulus was clearly dominant, also when a small part of the percept was mixed. Subjects were instructed not to press any button to indicate failed trials if: (a) dominance induction by flash suppression failed, (b) *any* spontaneous perceptual switch or *any* (even if small) piecemeal percept occurred prior to the interruption, (c) neither of the stimuli dominated following the interruption.

Experimental blocks consisted of 16 trials that were balanced for initial dominance side, stimulus side, and post-interruption eye exchange vs. no exchange and were presented in random order. Blocks of each of short (300 ms) and long (3000 ms) dominance durations prior to the interruption were run in counterbalanced order for each subject. In the experiment using flower stimuli, 5 subjects performed 8 blocks of each type; one did 5. In the experiment using grating stimuli, subjects performed at least 4 blocks of each type.

Onset rivalry

This followed the same procedure as above, but with simultaneous presentation of both flowers ([Figure 2a](#)). Subjects reported the initial percept by a first button press and the post-interruption percept by a second button press, both after the interruption pattern. Again, no or more than two button presses indicated failed trials with the same instructions as above. Subjects performed at least 12 blocks of each of long and short dominance trials.

Continuous rivalry

Blocks consisted of 3 min of continuous viewing ([Figure 5a](#)). During each dominant percept, subjects kept

the button of the corresponding stimulus depressed, also when it was interrupted by the brief interruption patterns, with no button pressed during piecemeal percepts. Interrupting patterns were presented either 300 ms or 3000 ms following the onset of a new dominant percept, with or without simultaneous stimulus exchange between the eyes, resulting in four types of blocks. Interruptions were only applied when no perceptual transition was reported during the respective preinterruption interval. To ensure a minimal consistency in perceptual history before interruptions, more than 4 s and two spontaneous (i.e., non-interruption induced) perceptual switches had to pass between subsequent interruptions, and the percept prior to the triggering perceptual switch had to last at least 1000 ms. Subjects performed at least 8 blocks of each type, resulting in at least 1 h and 36 min viewing time per subject. Reports of perceptual switches across all conditions peaked around 550 ± 130 ms after interruptions (see [Figure 5b](#) and [Supplementary Figure S3](#)). The percentages of a perceptual switch occurring in the interval of 80–800 ms after each interruption were quantified to obtain an indicator of perceptual stability for each of the four conditions.

Results

Both flash suppression and onset rivalry settings yielded similar results. For clarity, we denote the perceived image of the initially dominant stimulus I and the initially suppressed image $\sim I$. $p(I)$ is the percentage of valid trials in which I continues to be perceived after the interruption pattern, with $p(\sim I) = 100 - p(I)$. Correspondingly, $p(E)$ is the percentage of valid trials in which the same eye continues to be dominant after the interruption pattern, with $p(\sim E) = 100 - p(E)$. Invalid (failed) trials (e.g., trials with ambiguous percepts) were not further analyzed here but reported in the figures as percentage of failed trials.

Flash suppression

In flash suppression, after short dominance (0.3 s), the percept was very stable in the same-eye condition but tended to change in the exchanged-eye condition (same-eye $p(\sim I) = 16.0 \pm 2.9\%$ (mean \pm SE), exchanged-eye $p(\sim I) = 63.7 \pm 7.6\%$, $n = 6$ subjects). It was thus primarily the processes related to the eye of origin that determined the perceptual outcome—whichever stimulus was shown to the initially dominant eye became dominant ([Figure 1b](#)). Note however that the exchanged-eye results do not exactly mirror the same-eye results, as $p(\sim I)_{\text{exchange-eye}}$ is significantly smaller than $p(I)_{\text{same-eye}}$ ($t(5) = 2.57$, $p < 0.025$). This indicates a small but significant stabilizing

effect of the initial percept on the perceptual outcome. Thus, after short dominance, there was a strong tendency of the previously dominant eye to stay dominant, and a weaker tendency of the initial percept to stay dominant.

In contrast, after long dominance (3 s; equivalent to the median dominance time in continuous rivalry for these stimuli, see [Methods](#) section), the interruption tended to lead to a perceptual switch in both same-eye and exchanged-eye experiments (same-eye: $p(\sim I) = 70.6 \pm 7.6\%$ (mean \pm SE); exchanged-eye: $p(\sim I) = 61.1 \pm 6.2\%$). This indicates a switch-favoring influence of the initial percept, regardless of the eye of presentation. Note also the slightly higher $p(\sim I)_{\text{same-eye}}$ than $p(\sim I)_{\text{exchanged-eye}}$, indicative of an ocular factor favoring an eye switch (this survived only a one-tailed t -test with $t(5) = 2.20$, $p = 0.039$, but the important point is the significant *change* of the eye-based contribution, shown in the interaction of the ANOVA described below). Thus, after long dominance, there was a strong tendency of the initial percept to change and also a weaker tendency of the eye of origin to change. Therefore, over time, two independent factors changed: the eye-based as well as the percept-based stabilization decreased, both turning into destabilizing forces. [Supplementary Figure S2](#) shows the typical outcomes of this experiment in a graphical form.

Statistically, the change of the eye-based contribution over time is reflected in a significant interaction between the two factors “duration” and “eye” for $p(\sim I)$ (two-way ANOVA, $F(1, 20) = 20.09$, $p < 0.0002$, $n = 6$ subjects; each subject separately: $p < 0.05$). The main factors also achieved significance, in the group analysis (eye: $F(1, 20) = 8.98$, $p < 0.007$; duration: $F(1, 20) = 16.65$, $p < 0.001$), and in five out of six subjects with $p < 0.02$ each. Conversely, the change of the initial percept contribution over time is reflected in an interaction between “duration” and “percept” for $p(E)$. $p(E)$ equals $p(I)$ in same-eye conditions, and $p(\sim I)$ in exchanged-eye conditions. The interaction was significant with at least $F(1, 20) = 8.98$, $p < 0.007$ for both the flash suppression and the onset rivalry settings.

In sum, the data reveal that there is an early strong eye-of-origin stabilizing contribution that declines over time (turning from strongly stabilizing into weakly destabilizing), and similarly a higher level image/perceptual contribution that has first a small stabilizing effect and later a strong destabilizing effect.

Note that the data are indistinguishable in both exchanged-eye conditions ([Figure 1b](#), right column). This indicates that the amount of change in eye-of-origin and image contributions was identical, thus canceling each other in the exchanged-eye conditions at any given time.

Onset rivalry

To test replicability of these findings, we repeated the experiments in a second setting (onset rivalry) where

initial dominance was not experimentally predetermined ([Figure 2a](#)). The key findings were the same as in flash suppression, but with a stronger eye-based stabilizing contribution in all conditions. The ANOVAs reported for flash suppression held here with ($F(1, 20) = 9.54$, $p < 0.006$) in the group and $p < 0.05$ for 5 of 6 subjects. Thus, here too, the eye of origin had a greater stabilizing influence early than late in dominance. Again, the initial percept first had a weak stabilizing and later had a large destabilizing influence. This decrease of the image contribution over time was reflected in the interaction of duration and percept for $p(E)$ ($F(1, 20) = 9.54$, $p < 0.006$). Again the exchanged-eye conditions were indistinguishable for long and short trials, indicating that the changes of eye-of-origin and image contributions over time were equal and thus neutralized each other.

Replication with simple grating stimuli

In a third experiment, we used oriented gratings instead of flower stimuli in the flash suppression setting. Prior experiments have shown that suppression depth and also top-down (i.e., image to eye of origin) modulation in rivalry can depend on stimulus complexity and on the amount of shared neural substrate between the stimuli (Alais & Melcher, 2007; Knapen et al., 2007; Ngo et al., 2007; van Boxtel et al., 2008; Watson et al., 2004). We were thus curious to find out whether a flash suppression experiment using simple gratings would replicate the results obtained using the more complex flower stimuli.

[Figure 3](#) shows that the results were replicated in that factors “eye,” “duration,” and their interaction each achieved significance in a 2-way ANOVA just as in the two preceding experiments (duration: $F(1, 32) = 19.29$, $p < 0.0001$; eye: $F(1, 32) = 8.93$, $p < 0.006$; interaction: $F(1, 32) = 5.16$, $p < 0.03$, $n = 9$ subjects), as did the interaction in the ANOVA of $p(E)$ using the factors “percept” and “duration” ($F(1, 32) = 8.93$, $p < 0.006$). Thus, eye of origin as well as image contributions declined over time, with very similar values as obtained using the flower stimuli. Interestingly, the only difference relative to Experiment 1 was that the exchanged-eye conditions were not exactly equal for 0.3 and 3 s trials ($t(17) = 2.61$, $p < 0.02$), showing that the *changes* in influences related to the eye of origin and to the initial percept over time were not exactly equal with grating stimuli, thus failing to cancel each other completely in the exchanged-eye conditions. A 3-way ANOVA with the factors (stimulus, eye, duration) confirmed an effect of stimulus type in the interaction between stimulus and duration for $p(E)$ ($F(1, 52) = 4.36$, $p < 0.042$). It is unclear though whether this small difference is accounted for by the difference in high-level stimulus content, or by other differences between flower and grating stimuli, such as the different contrast and spatial frequency content, or because different subjects were tested.

Flash suppression: grating stimuli

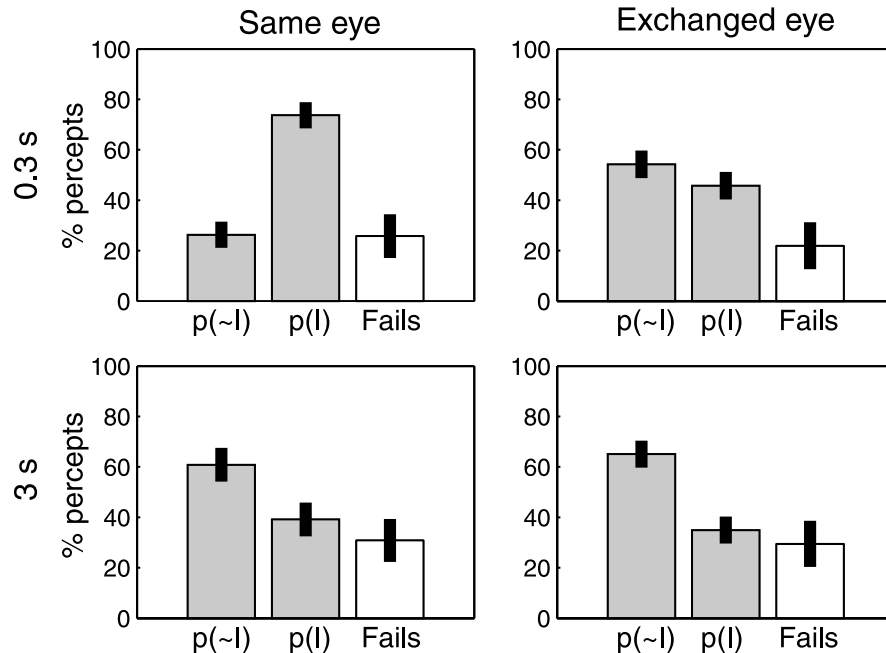


Figure 3. Replication of Experiment 1 with grating stimuli. All findings of Experiment 1 were replicated. In addition, there was a small but significant difference here between exchanged-eye conditions at 0.3- and 3-s dominance.

Finally, note that in the grating experiments subjects responded to the shape, not the hue, of the gratings. Our findings thus certainly apply to shape cues. Note also that none of the subjects observed color rivalry independently of shape in any of the experiments. Indeed, [Supplementary Figure S3](#) shows that results can be replicated using black-and-white grating stimuli alone (shown for 3 subjects).

Gradual change over time

In order to determine whether the observed effect of change in the strengths related to the eye of origin and to the initial percept developed gradually over time, we tested four observers at dominance durations of 0.3, 1, 2, and 3 s, two with flash suppression, and two in onset settings. [Figure 4](#) shows that the change occurred linearly over time. The same-eye conditions reveal a steady increase of perceptual switches, while the exchanged-eye conditions reveal a constant switch frequency across dominance durations. These results indicate a gradual and concurrent weakening of both, the stabilizing contribution of the initially dominant eye as well as of the initially dominant percept, such that both changes neutralize each other in eye-exchange conditions.

Continuous rivalry

Finally, we attempted to characterize the effects observed above in free-running rivalry lasting several

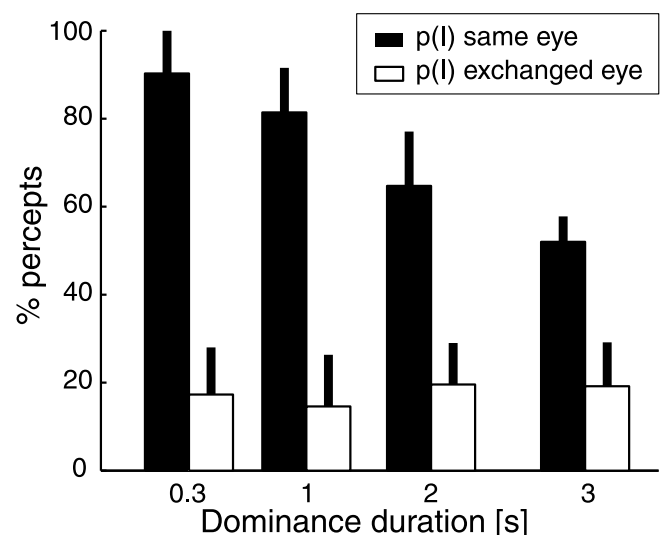


Figure 4. Time resolved data of the effect shown in the previous experiments. Each bar shows $p(l)$ of a full experiment, conducted with 0.3-, 1-, 2-, and 3-s initial dominances, and with stimuli shown to the same eyes (black) or exchanged eyes (white) after the interruption. Over time, a linear decrease of perceptual stability in same-eye conditions is apparent. In the exchanged-eye conditions, no change happens, as the changes due to eye of origin and due to initial percept are equally large and cancel each other ($n = 4$, error bar: SEM).

minutes. We applied interruption patterns after 0.3 s or 3 s (with and without eye swaps) following reports of a perceptual switch during continuous rivalry (see [Methods](#) section and [Figure 5a](#)). In total, the viewing time across the eight subjects summed to more than 20 h. Across all subjects, the interruptions led reliably to perceptual switches in all conditions, evident in the histogram of [Figure 5b](#) showing a total of 5230 reported perceptual switches within the interval of 0–2 s following interruption pattern presentations, with a clear peak around 530 ms ([Supplementary Figure S4a](#) shows switch histograms for the four conditions separately). The probability that an interrupting pattern induced a perceptual switch (i.e., $p(\sim I)$) was significantly modulated by both factors “eye” ($F(1, 28) = 17.23, p < 0.000, n = 8$) and “duration” ($F(1, 28) = 5.42, p < 0.027$) in a 2-way ANOVA across the group of eight subjects (within the interval of 80–800 ms) and is shown in [Figure 5c](#). Seven out of eight subjects reached significance for the factor “eye” and four subjects for “duration” ($p < 0.05$). There were significant interactions between duration and eye exchange in five out of the eight subjects with $p < 0.05$ indicating a time dependence of eye-exchange effects in the majority of subjects. However, in contrast to the trial-based experiments that had a better controlled percept history, the sign of the interactions differed from subject to subject, thus preventing significance of this interaction across the group. [Supplementary Figure S4b](#) shows percentages of post-interruption switches for three subjects representative for the three types of effects found in continuous rivalry, with positive, negative, and no interaction. Thus, while continuous rivalry revealed significant main effects of time and eye exchange, their interaction varied across subjects. It is likely that the complex and uncontrolled stimulus histories as well as attentional fluctuations during the long viewing time in this paradigm account for the higher variability within and across subjects. Indeed, factors varying at very slow time scales have been shown in prior studies to affect switch frequencies in continuous rivalry (Brascamp et al., 2008; Klink et al., 2008; Ngo et al., 2007; Ooi & He, 1999).

Discussion

This study used a novel experimental paradigm to estimate the degree to which processes related to the eye of origin and to image content contribute to binocular rivalry at precise time points during a dominance phase. While the stabilization of the eye of origin as well as of that of the initial percept differed in magnitude, we found that both contributions declined over time, eventually leading to a destabilization. At the initial stages of dominance (0.3 s), both contributions were of a stabilizing nature: a given dominant eye tended to remain dominant

(no matter which stimulus was shown to it), and a given dominant image tended to remain dominant (no matter through which eye it was seen). This stabilization declined over time and turned negative after a longer period of dominance: a given dominant eye tended to become suppressed (independent of the stimulus presented to it), and a given dominant image tended to change (independent of the eye of presentation). The magnitude of the *change* of the eye-of-origin channel and of the perceptual channel appeared to be matched, such that the results were identical in eye-exchanged conditions, when eye- and image-based contributions cancelled each other. Thus, eye- and image-based contributions declined in parallel over time.

Because the stabilizing contribution of the eye of origin was larger, it was first the image-based contribution that crossed the zero line and destabilized the current percept.

Our findings thus offer a qualitative and quantitative addition to the consensus that binocular rivalry involves contributions from both processes related to the eye of origin as well as those related to the stimulus/percept by showing that the influences of both appear to co-vary over time, even if their absolute contributions can differ in magnitude at any given time (Alais & Melcher, 2007; Bhardwaj et al., 2008; Blake & Logothetis, 2002; Knapen et al., 2007; Ngo et al., 2007; Pearson & Clifford, 2004; van Boxtel et al., 2008; Watson et al., 2004).

The effect of eye swaps

One key study that has been taken to provide evidence for an eye-based contribution to perceptual dominance in rivalry was by Blake et al. (1980). They showed that swapping stimuli between the eyes after subjects reported stable dominance tended to lead to a perceptual switch, thus showing that the percept followed the initially dominant *eye*. The authors carefully also included “non-swap” trials in which both rival targets were briefly turned off and then on without exchanging stimuli between the eyes—those trials did not produce abbreviated dominance durations. These results essentially correspond to those obtained in our short (0.3 s) dominance trials and were correctly interpreted as eye-dominated perception, in which the percept follows the dominant eye.

Had Blake et al. (1980) allowed for longer dominance periods prior to swapping stimuli between eyes, a very different result and interpretation would have emerged: namely that the percept changes regardless of the eye of presentation. This was evidenced in our long (3 s) dominance trials: the percept switched in both eye-swap as well as non-swap trials. Thus, late in dominance it was primarily the dominant stimulus that determined the percept (by destabilizing it), with no or very little influence of the dominant eye.

It is important to note that following an eye swap the percept tends to change after both short and long

a Continuous rivalry:

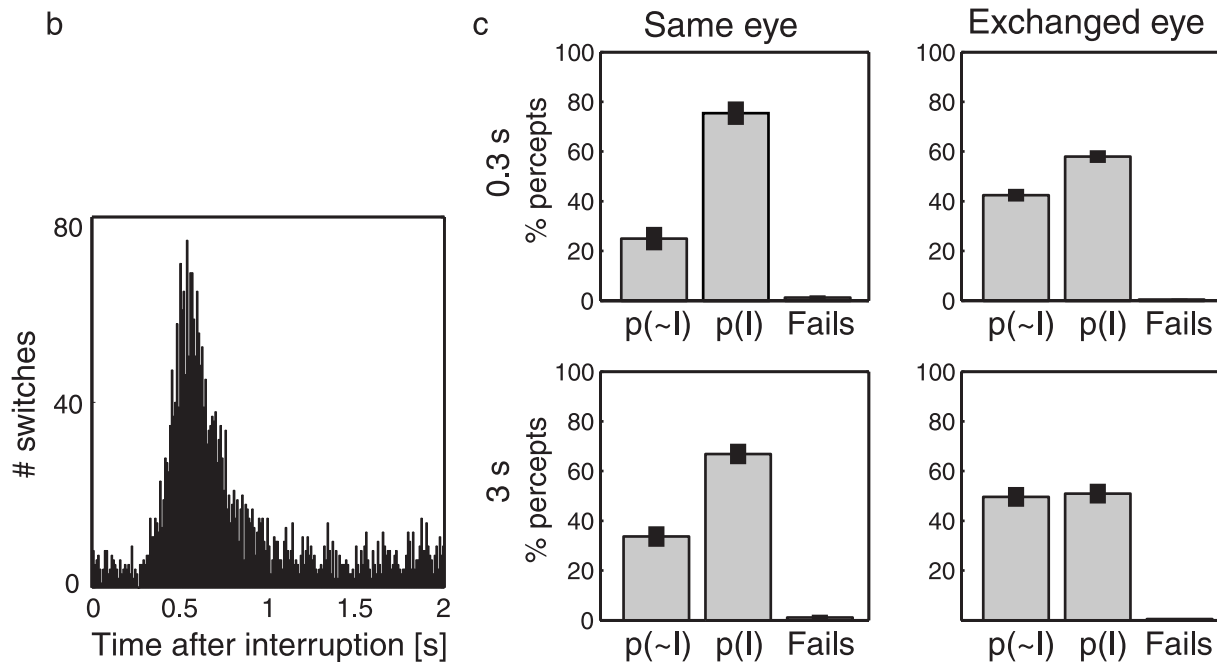
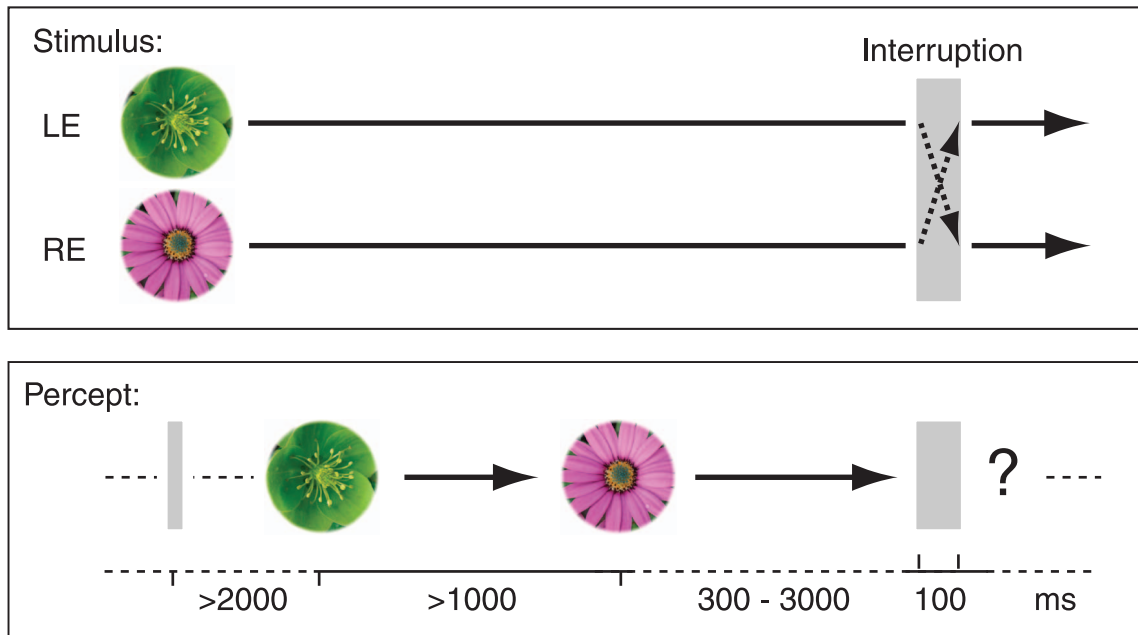


Figure 5. Stimuli and results from the continuous rivalry experiment. (a) In several viewing sessions lasting 3 min each, interrupting patterns were presented either 0.3 or 3 s after a spontaneous perceptual transition. Conditionals for interrupting pattern presentations were a minimal inter-interruption interval of 4 s and two intermittent spontaneous perceptual transitions, and a stable percept for at least 1 s prior to an interruption-triggering transition. (b) Histogram of perceptual switches after binocular interruption pattern presentation during continuous rivalry. Data are pooled from all sessions and conditions across all 8 subjects and include 5230 reported switches in the interval shown. Bin size = 10 ms (see [Supplementary Figure S4](#) for histograms of separate conditions). (c) Perceptual outcomes during continuous rivalry (with switches quantified within 80 and 800 ms of the interruption). Across subjects, switch frequencies were significantly affected by time and eye exchange (2-way ANOVA: $p < 0.05$, $n = 8$), but with interactions reaching significance only at the single-subject level in five out of eight subjects (see also [Supplementary Figure S4b](#)).

preceding dominance periods, but for entirely different reasons: after short dominance, the percept switches as it follows the dominant eye, and after long dominance it switches because of the interruption inherently associated to an eye swap at the monocular level. Providing the interruption alone therefore tends to induce a perceptual switch after long dominance, also without an eye swap.

Therefore, our results reveal two apparently separate factors related to eye and to stimulus whose contributions change throughout a given dominance period.

One approach to emphasize percept rivalry consists of rapid repetitive stimulus flicker combined with rapid repetitive eye swapping (Lee & Blake, 1999; Logothetis et al., 1996; Pearson et al., 2007; Wilson, 2003). During this so-called swap rivalry, dominant percepts can survive across several eye swaps (Logothetis et al., 1996), showing that rivalry is not only dependent on competition between signals related to the eyes. Beyond *revealing* percept rivalry, this paradigm has been suggested to actually emphasize percept rivalry relative to eye rivalry (Lee & Blake, 1999; Wilson, 2003). Bhardwaj et al. (2008) found that monocular probes were more easily detected during swap rivalry (image rivalry) compared to normal rivalry (eye + image rivalry) thus concluding that eye rivalry mediates deeper suppression than image rivalry (Bhardwaj et al., 2008). Because the probes in Bhardwaj's experiment appear to have been shown early within dominance phases, it is compatible with our finding of a stronger (stabilizing) contribution of eye-based factors compared to perceptual ones early during a dominance phase. However, it would be interesting to learn the result of Bhardwaj's approach late in dominance as well, as the outcome may vary with dominance duration as shown here.

Swap rivalry constitutes a very particular regime that repetitively (3 Hz) interferes with processes occurring during normal rivalry in unknown ways (e.g., interactions between processes related to the current percept and those related to the eye of origin). It is likely that the repetitive eye swaps during swap rivalry deemphasize eye rivalry rather than emphasize percept rivalry, as suggested by modeling (Wilson, 2003). This may partly explain the discrepancy between swap rivalry (thought to emphasize percept rivalry) and our result showing highest eye-of-origin contribution early in dominance (e.g., 0.3 s after dominance), because our experiments also revealed the highest stabilizing contribution of image-based factors early in dominance, in accord with swap rivalry. A selective reduction of the eye-based contribution due to the 3-Hz swap would thus reveal the strong stabilizing image contribution early in dominance. In contrast to swap rivalry, the interruption paradigm employed here did not interfere with the dominance phase preceding the probe, thus allowing the measurement of eye-based and image-based contributions following undisturbed dominance phases, with the only manipulation being the probe

itself. The effects of the probe are discussed in the following.

The effect of interruptions and paradigms

While brief stimulus interruptions have been shown to induce perceptual switches (Blake & Fox, 1974; Kornmeier & Bach, 2005; Orbach, Zucker, & Olson, 1966), also as a function of preceding dominance time (Kanai et al., 2005), very long interruptions (in the range of seconds) tend to stabilize the percept, forming a so-called percept memory over seconds and even minutes (Klink et al., 2008; Leopold et al., 2002; Orbach, Ehrlich, & Heath, 1963).

Paradigms similar to the one used here but using interruptions lasting several seconds showed that the percept memory depended only partly on binocular stimulus features but primarily on the retinal location and eye of origin (Chen & He, 2004; Pearson & Clifford, 2004). This allowed models of competition and adaptation at low levels to capture this process, which may have its own dynamics (Brascamp, Pearson, Blake, & van den Berg, 2009; Noest, van Ee, Nijs, & van Wezel, 2007). In contrast to such long interruptions, the isolated brief interruptions applied here tended to destabilize rather than stabilize the predominant percept or ocular channel, and these effects strongly depended on the preceding dominance time. Like others, we thus suggest that brief interruptions are useful for probing the state of the system, yielding indications of the stabilizing or destabilizing contribution of ocular or perceptual contributions to rivalry, and especially of time-dependent changes thereof (Kanai et al., 2005).

Nevertheless it should be noted that the brief interruptions may themselves—in addition to probing the system—additionally add an offset to the results. This offset would, however, be equal across all conditions, because the interruption was always the same, with the only changing variables being the stimuli surrounding the interrupting probe (and hence the state of the neural system).

For example, our finding that the eye-based contribution had a greater stabilizing strength in onset rivalry compared to flash suppression (compare Figures 1 and 2) indicates a considerable influence of the paradigm or of the perceptual history. In flash suppression, the dominant eye and stimuli were induced and counterbalanced by the experimenter, while in onset rivalry the initial dominance was determined largely by eye-based factors that preceded the stimulus presentation, as described by Carter and Cavanagh (2007). Thus, the observed positive offset of the stronger eye-based stabilizing contribution in onset rivalry reveals that onset rivalry is governed by a stronger eye-based contribution compared to flash-suppression-induced dominance. One factor additionally contributing to this

may be the difference in stimulus history: in flash suppression, the suppressed eye was adapted 500 ms longer to a stimulus than the dominant eye. Despite these differences both paradigms revealed the same dynamics, with both eye-based and image-based stabilizing contributions decreasing over time, until they turn into destabilizing forces that most likely would eventually account for the spontaneous perceptual switch.

One potential reason for the difference in results between trial-based and continuous rivalry experiments may lie in the comparably complex and uncontrolled stimulus history in the continuous rivalry experiments. Recent studies have revealed that long-term perceptual (and ocular) history affects rivalry with variables governed by very slow time scales that may have been imbalanced across conditions in continuous rivalry experiments (Brascamp et al., 2008; Klink et al., 2008; Ngo et al., 2007; Ooi & He, 1999). In addition, there is evidence that dominance in trial-based rivalry may differ also in other aspects from that of continuous rivalry, e.g., as explained above in the examples of flash suppression and onset rivalry (Blake, Westendorf, & Fox, 1990; Carter & Cavanagh, 2007; Tsuchiya, Koch, Gilroy, & Blake, 2006).

Interactions between eye-based and perceptual processing stages

The result with potentially the most far-reaching implications is that both eye-based and image-based contributions varied to the same extent over time. It reveals dynamics that is common to both, suggesting that the strength of one may affect the strength of the other, implying a direct interaction between the two. These results may thus be helpful to constrain models of binocular rivalry (Freeman, 2005; Noest et al., 2007; Wilson, 2003).

This finding is also consistent with prior experiments demonstrating perceptual influences on eye-based processing stages. For example, rivalry experiments have shown that the monocular afterimage associated to the dominant percept is stronger than the afterimage of the previously suppressed percept, implying interactions of perceptual with monocular representations (Gilroy & Blake, 2005; Tsuchiya & Koch, 2005). Similarly, the finding that dichoptically presented point-like walkers tend to rival, whereas eye-scrambled ones do not, suggests that high-level processes interact with suppression of eye-based signals (Watson et al., 2004). Finally, there is ample evidence for attentional top-down as well as bottom-up processes influencing dominance in rivalry (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999; Paffen, Alais, & Verstraten, 2006).

In fact, the curious dissociation between spiking activity and local field potentials (as well as with fMRI signals)

observed in early visual stages during rivalry has been related to feedback from higher cortical processing stages (Gail, Brinksmeier, & Eckhorn, 2004; Haynes, Deichmann, & Rees, 2005; Keliris, Logothetis, & Tolias, 2010; Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; Maier et al., 2008; Wilke, Logothetis, & Leopold, 2006; Wunderlich, Schneider, & Kastner, 2005). Spike-rate modulations in LGN and V1 during rivalry tend to be very modest (affecting 15–20% of neurons, and those only to a small degree; Gail et al., 2004; Keliris et al., 2010; Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; Wilke et al., 2006), with much higher modulations in higher stages (strongly affecting >50–90% of neurons; Brouwer & van Ee, 2007; Lehky & Maunsell, 1996; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). In contrast, local field potentials as well as fMRI signals revealed robust modulations also in V1 (Gail et al., 2004; Haynes et al., 2005; Maier et al., 2008; Wilke et al., 2006; Wunderlich et al., 2005). It has been hypothesized that the dissociation between spiking activity and LFP/BOLD signal during rivalrous suppression may result from feedback of higher level areas to V1, which may affect LFPs more than spiking activity (Maier et al., 2008; see also Bartels, Logothetis, & Moutoussis, 2008; Logothetis, 2008). Indeed, laminar LFP recordings support this notion, as they revealed perceptually modulated changes in membrane currents within the upper layers of V1 that receive recurrent feedback from higher cortical areas (A. Maier (NIH/NIMH), personal communication). Since neural representations retaining eye-of-origin information can be found throughout the visual system (Burkhalter, Felleman, Newsome, & Van Essen, 1986; Maunsell & Van Essen, 1983; Uka, Tanaka, Yoshiyama, Kato, & Fujita, 2000), image- and eye-based interactions could in principle occur also at higher stages.

Given the complexity of neural processing and the large array of interconnected brain regions involved in rivalry, mechanistic accounts can at most be tentative. Nevertheless, the steady time-dependent decrease of both stimulus- and eye-of-origin stabilizing contributions makes adaptation a plausible contributor to our findings (together with noise, inhibition, etc). Adaptation has been proposed in various models of rivalry (Laing & Chow, 2002; Lehky, 1988; Noest et al., 2007; Wilson, 2003), and there is good evidence that monocular adaptation periods inserted into ongoing rivalry can alter perceptual switches in ways compatible with our findings (Kang & Blake, 2010). However, other models based on attractors and noise appear to be able to account for rivalry similarly well (Kim, Grabowecky, & Suzuki, 2006; Moreno-Bote, Rinzel, & Rubin, 2007), and our findings provide no direct reason to prefer one model over the other apart from being compatible with fatigue-related processes. Because neurons at higher cortical stages (as opposed to those in V1 or LGN) are strongly modulated by the dominant percept, adaptation may conceivably occur with increasing dominance times. Whether due to adaptation or not,

changes in higher level activity may affect the underlying eye-of-origin representations, either by affecting excitability or by processes not affecting spike rates but population synchrony or noise levels instead (Cohen & Maunsell, 2009; Mitchell, Sundberg, & Reynolds, 2009; Schurger, Pereira, Treisman, & Cohen, 2010).

While our analyses revealed overall very similar results for flower stimuli and orientated gratings, there was a reduction in the eye-based change over time for the gratings. If confirmed in future experiments, this may be indicative of reduced interactions between percept and eye-related representations during exposure to simple stimuli, potentially due to less rivalrous interactions at higher levels of processing (Alais & Melcher, 2007; Knapen et al., 2007). At present, however, alternative explanations (such as differing stimulus contrast, luminance or spatial frequency content, etc.) cannot be excluded to account for the small difference in results. This leaves us with the conclusion that both complex and simple stimuli are governed by a similar dynamics, which in turn may reflect interactions between eye-based and perceptual neural processing stages.

Conclusions

Our paradigm allowed us to obtain a time-resolved measure of eye-of-origin and image-based contributions to perception during binocular rivalry. The results demonstrate that both contributions vary over time: the stabilizing contribution of both declined in parallel during the dominance phase in rivalry. Our findings may thus provide an account for the dynamics underlying perceptual switches in rivalry. The co-variation of eye-based and perceptual contributions over time, combined with the latest evidence from physiology, lead us to suggest that feedback from high-level percept representations may affect the strength of the eye-of-origin contribution to dominance. It is this dynamic interaction that may underlie the perceptual alternation observed in rivalry, but also other bistable perceptual phenomena (Andrews & Purves, 1997; Blake & Logothetis, 2002; Purves & Lotto, 2003; Sindermann & Luddeke, 1972). In fact, the special case of binocular rivalry may merely reveal a capacity—namely time-evolving neural interactions between high- and low-level neural stimulus representations—that may underlie much of normal perception.

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